A Synopsis of *Tropidocarpum* (Brassicaceae)

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ABSTRACT. *Twisselmannia californica* is transferred to *Tropidocarpum* (Brassicaceae). A key to the four species of *Tropidocarpum* is presented. Disjunction between the North and South American species of the genus is discussed.

Key words: *Agallis*, Brassicaceae, fruit diversity, *Tropidocarpum*, *Twisselmannia*.

As presently delimited, *Tropidocarpum* Hooker (Brassicaceae) consists of four species, of which *Twisselmannia californica* Al-Shehbaz and *Agallis lanata* (Barnéoud) Gilg & Muschler ex O. E. Schulz were previously placed in monotypic genera. The narrowly endemic *T. californica* is restricted to a limited number of scrub habitats in the Central Valley of California (Al-Shehbaz, 1999). Although *Twisselmannia* Al-Shehbaz was reduced to synonymy of *Tropidocarpum* by Appel and Al-Shehbaz (2002), formal transfer of its species to *Tropidocarpum* was not proposed. *Agallis lanata* is very rare and occurs disjunctly in central Chile in habitats similar ecologically to those where species of *Tropidocarpum* grow. It was transferred to *Tropidocarpum* by Al-Shehbaz and Price (2001). Of the other two species originally assigned to *Tropidocarpum*, *T. gracile* Hooker is a relatively widespread and abundant species occurring in open habitats and lower montane slopes from Baja California north to central California (see below), whereas *T. capparideum* Greene is an extremely rare species previously known only from the vicinity of Mt. Diablo in the San Francisco Bay area of California (Rollins, 1993a, 1993b). *Tropidocarpum capparideum* was not collected for nearly 45 years and was last seen in 1957 and presumed extinct (Rollins, 1993b). However, the species has been collected in 2000 by Meredith Osborne (CDA) and in 2001 by Fred Hrusa (CDA) and Dieter Wilken (SBBG). These collections, all cited below, were made from Fort Hunter Liggett in Monterey County, and I have confirmed their identity.

All four species are annuals with a remarkably similar morphology, especially in their indumentum (with coarse simple trichomes mixed with smaller forked ones), petiolate and pinnatisect to pinnatifid cauline leaves, racemes bracteate throughout, yellow flowers occasionally tinged with purple, staminal filaments with dilated bases, angustiseptate fruits (flattened at a right angle to the septum), mucilaginous seeds, and incumbent cotyledons. However, they have drastically different fruits (Fig. 1). *Twisselmannia* has a very distinctive obdeltoid silicle (4–5 × 3–4 mm) with leathery-thickened and tuberculate-rugose valves, whereas *Tropidocarpum gracile* has narrowly linear siliques up to 7 cm × 2 mm. Both *T. capparideum* and *T. lanatum* (Barnéoud) Al-Shehbaz & R. A. Price have oblong fruits, but the former has four rather than two valves, a condition rarely seen elsewhere within the Brassicaceae (Al-Shehbaz, 1984).

Molecular studies of *Twisselmannia californica*, *Tropidocarpum gracile*, and *T. lanatum* (Price, unpublished) demonstrate that the three species are almost identical in sequence, differing by only 1 or 2 base pair substitutions, for the chloroplast gene *ndh*F and the nuclear ribosomal DNA ITS region. The three species form a monophyletic clade, with 100% bootstrap support, and this clade is weakly separated (54% bootstrap support) from a monophyletic *Descurainia* Webb & Berthelot including *Hugueninia* Reichenbach (Price, unpublished). Because of the extremely small amount of sequence divergence observed among the three species for the rapidly changing *ndh*F and ITS regions, it appears that both the drastic change in fruit shape between *Twisselmannia* and its *Tropidocarpum* congeners and the North American–South American disjunction involving *T. lanatum* are relatively recent events in the history of the Brassicaceae.

Fruit and seed morphology have traditionally been heavily emphasized in generic and tribal classification of the Brassicaceae (Hedge, 1976; Al-Shehbaz, 1984), but recent molecular phylogenetic studies suggest that fruit and seed morphology have been subject to frequent homoplasy (Koch et al., 1999, 2001) and that many of the commonly recognized tribes in the family are highly artificial.

Remarkable differences in fruit morphology are found in several other genera of the Brassicaceae. For example, *Rorippa* Scopoli (ca. 75 spp., distributed worldwide) has fruits ranging from narrowly

linear to oblong or globose and with two or rarely three to six valves (Appel & Al-Shehbaz, 2002). Another striking example of fruit diversity is found in *Vella* L., a genus of seven species of shrubs endemic to Algeria, Morocco, and Spain (Appel & Al-Shehbaz, 2002). All species of *Vella* have segmented, 1- to 8-seeded fruits, connate median staminal filaments, and a base chromosome number of $x = 17$ (Warwick & Al-Shehbaz, 1998). One species, *V. bourgaeana* (Cosson) Warwick & Al-Shehbaz, previously treated as the monotypic genus *Euzomodendron* Cosson (López González, 1993), has linear-lanceolate fruits and seeds broadly winged all around, whereas the remaining species have globose to ellipsoid fruits and seeds with vestigial wings. Molecular data (Warwick & Black, 1994; Crespo et al., 2000) clearly show that *Euzomodendron* is nested within *Vella*, and thus they form a monophyletic genus. Several other genera of Brassicaceae show very wide ranges of fruit morphology. These include *Draba* L. (Schulz, 1936), *Heliophila* L. (Marais, 1970), *Graellsia* Boissier (Poulter, 1956), *Isatis* L. (Davis, 1964), *Leavenworthia* Torrey (Rollins, 1963), *Ornithocarpa* Rose (Rollins, 1969), and *Sphaerocardamum* Schauer (Bailey, 2001).

The almost identical sequence similarity between *Twisselmannia* and species of *Tropidocarpum* contrasts with the apparent rapidity with which major changes in fruit morphology can sometimes occur among closely related taxa. A classic example of a similar situation was elucidated earlier by Sytsma and Gottlieb (1986) in the evolution of the strikingly divergent *Heterogaura* from within the genus *Clarkia* Pursh (Onagraceae). It would be particularly interesting to conduct comparative genetic and developmental studies of the fruits of *Tropidocarpum*, including *Twisselmannia*.

Another interesting aspect of the genus *Tropidocarpum* is the large disjunction between the Mediterranean climate zones of California and Chile (Fig. 1), which was unrecognized until Al-Shehbaz and Price (2001) transferred *Agallis lanata* to *Tropidocarpum*. The pattern of disjunction among species of many genera between these environmentally similar areas of North and South America was elegantly covered by Raven and Axelrod (1978).

KEY TO THE SPECIES OF *TROPIDOCARPUM*

1a. Fruits obdeltoid, spreading or antrorsely hirsute, 4- to 8-seeded; valves thick leathery, tuberculate-rugose distally . . . . . *T. californicum*
1b. Fruits linear, oblong, or elliptic, retrorsely hirsute (except when glabrescent), 16- to 70-seeded; valves thin-leathery, smooth.
  2a. Fruits narrowly linear, (2.5–)3–6(–7) cm × 1.5–2 mm . . . . . *T. gracile*
  2b. Fruits oblong to elliptic, 1–2(–2.5) cm × 3–5 mm.
    3a. Fruit valves 4; anthers oblong, 0.4–0.5 mm; fruit 25- to 40-seeded; California . . . . . *T. capparideum*
    3b. Fruit valves 2; anthers ovate, 0.15–0.25 mm; fruit 16- to 26-seeded; Chile . . . . . *T. lanatum*

1. Tropidocarpum californicum (Al-Shehbaz) Al-Shehbaz, comb. nov. Basionym: *Twisselmannia californica* Al-Shehbaz, Novon 9: 132. 1999. TYPE: U.S.A. California: Kings Co., S of Kettleman City, E side of Interstate Hwy. 5, 3 mi. N of Kern Co. line, grazed valley saltbush scrub, 30 Mar. 1994, *Ed LaRue s.n.* (holotype, UCR).

Distribution. U.S.A. California: Kings County.

Specimens examined. U.S.A. **California:** Kern Co., Kern National Wildlife Refuge, *Twisselmann 10447* (CDA); Kings Co., ca. 13 mi. S of Kettleman City, along pipeline access road lying 0.3 mi. E of Interstate 5, 3.1 mi. N of Kern Co. line, *Taylor 17098 & Ertter* (MO, UC).

To my knowledge, the collections above represent all that is known for the species.

2. Tropidocarpum capparideum Greene, Pittonia 1: 217. 1888. TYPE: U.S.A. California: [Contra Costa Co.], alkaline valley lands skirting the San Joaquin River, [Byron Springs], 25 Mar. 1888, *E. L. Greene s.n.* (holotype, NDG 02806).

Distribution. U.S.A. California: Contra Costa and Monterrey Counties.

Specimens examined. U.S.A. **California:** Contra Costa Co., Byron Hot Springs, *Hoover 806* (MO); Monterry Co., Fort Hunter Liggett, adjacent to Gabilan Road, ca. 0.8 mi. SSE of intersection with San Migelito Loop, *Hrusa 15805, with Wilken & Hazebrook* (CDA, MO), *Osborne 16, with Guzman & Witmore* (CDA, MO), *Hrusa 15804, with Wilken & Hazebrook* (CDA, MO); W of Gabilan Creek, ca. 0.4 km S of junction of Gabilan and San Migelito Loop roads, *Wilken 15876, with Morosco* (MO, SBBG).

The single specimen in Greene's herbarium collected in March 1888 was from Byron Springs, a locality not given in the original publication of the species. This specimen is taken herein as the holotype.

3. Tropidocarpum gracile Hooker, Icon. Pl. t. 43. 1836. TYPE: U.S.A. California: Monterey Co., Monterey, *David Douglas s.n.* (holotype, K).

Distribution. Mexico. Northern Baja California. U.S.A. California: Inner Coastal Range, Cascade

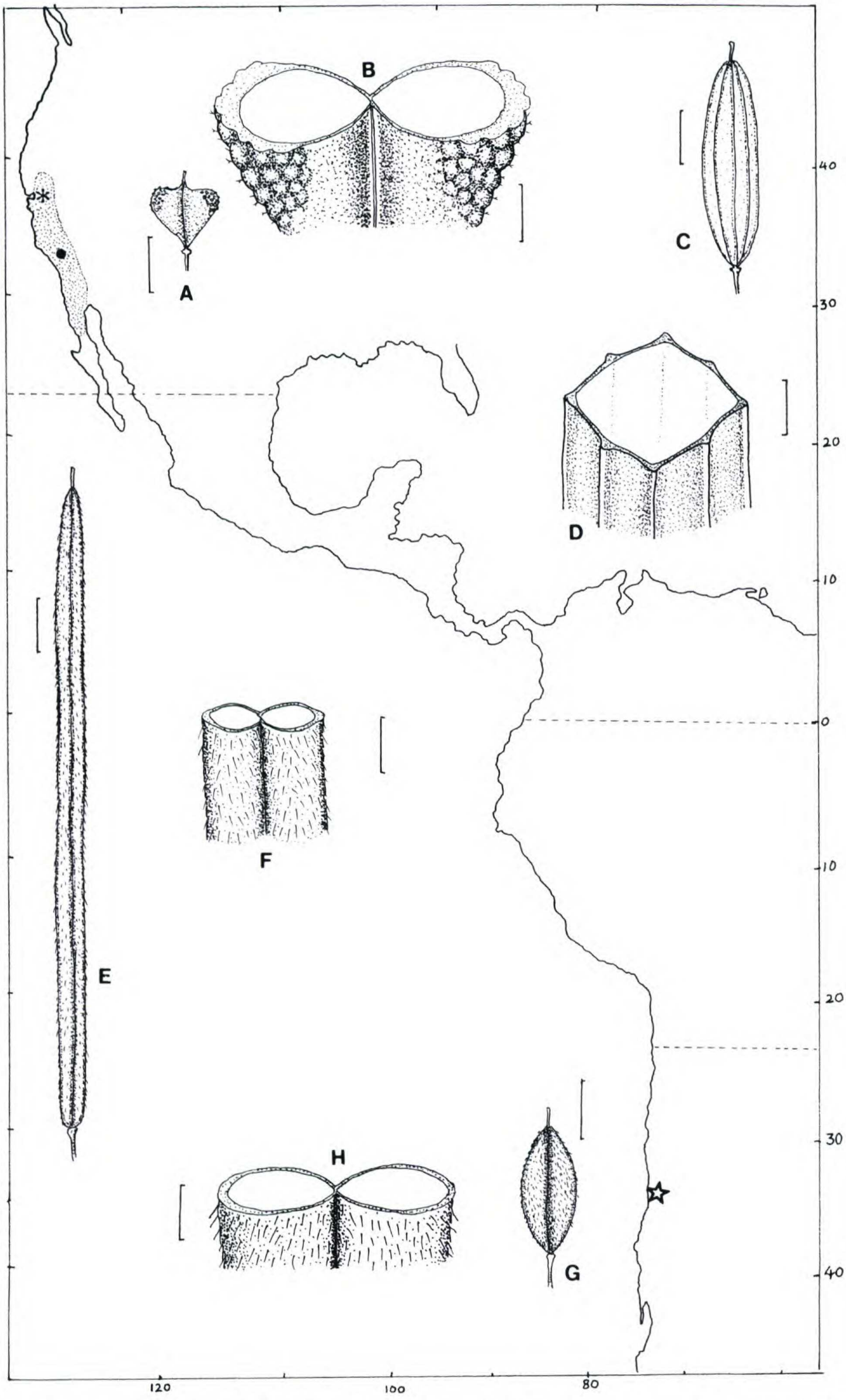

Figure 1. Fruits and distributions of *Tropidocarpum* species. —A, B. *T. californicum* (dot on map). —C, D. *T. capparideum* (asterisk). —E, F. *T. gracile* (stippled area). —G, H. *T. lanatum* (star). Cross sections in B, D, F, and H are made in widest portion of fruit. Scale: A, C, E, G = 5 mm; B, D, F, H = 1 mm. Dotted lines represent Tropic of Cancer, Equator, and Tropic of Capricorn. Drawn by Al-Shehbaz: A, B from *LaRue s.n.* (holotype, UCR); C, D from *Hoover 806* (MO); E, F from *Blankinship s.n.* (MO); G, H from *Claude Joseph 2791* (US).

Range foothills, Tehachapi Mountain, Great Central Valley, San Francisco Bay Area, Inner South Coast Range, Southwest California, and western Mojave Desert (Rollins, 1993b).

Specimen examined. U.S.A. **California:** Lake Co., Mt. Konocti, 29 Apr. 1929, *Blankinship s.n.* (MO).

4. Tropidocarpum lanatum (Barnéoud) Al-Shehbaz & R. A. Price, Novon 11: 293. 2001. Basionym: *Lepidium lanatum* Barnéoud, in Gay, Fl. Chile 1: 167. 1846. TYPE: Chile. Santiago, *C. Gay s.n.* (holotype, P; photos, F, US).

Distribution. Chile, Región IV and Región Metropolitana.

Specimens examined. CHILE. **Región IV:** Fray Jorge, Las Papas, *Jiles 720* (S); Ovalle, Bosque Fray Jorge, *Sparre 3029* (S). **Región Metropolitana:** Santiago, *Claude-Joseph 2232, 2267* (US); Lo Prado, *Claude-Joseph 2791* (US).

The above collections are the only ones known for the species, and the latest, *Jiles 720,* was made on 22 August 1948. No more recent collections are known for the species.

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Literature Cited

Al-Shehbaz, I. A. 1984. The tribes of Cruciferae (Brassicaceae) in the southeastern United States. J. Arnold Arbor. 65: 343–373.

———. 1999. *Twisselmannia* (Brassicaceae), a remarkable new genus from California. Novon 9: 132–135.

——— & R. A. Price. 2001. The Chilean *Agallis* and Californian *Tropidocarpum* (Brassicaceae) are congeneric. Novon 11: 292–293.

Appel, O. & I. A. Al-Shehbaz. 2002. Cruciferae. Pp. 75–174 *in* K. Kubitzki (editor), The Families and Genera of Vascular Plants, 5. Springer-Verlag, Berlin–Heidelberg.

Bailey, C. D. 2001. Systematics of *Sphaerocardamum* (Brassicaceae) and Related Genera. Ph.D. Dissertation, Cornell University, Ithaca, New York.

Crespo, M. B., M. D. Lledo, M. F. Fay & M. W. Chase. 2000. Subtribe Vellinae (Brassiceae, Brassicaceae): A combined analysis of ITS nrDNA sequences and morphological data. Ann. Bot. 86: 53–62.

Davis, P. H. 1964. Materials for the Flora of Turkey: VIII. Cruciferae. I: *Isatis.* Notes Roy. Bot. Gard. Edinburgh 26: 11–25.

Hedge, I. C. 1976. A systematic and geographical survey of the Old World Cruciferae. Pp. 1–45 *in* J. G. Vaughan et al. (editors), The Biology and Chemistry of the Cruciferae. Academic Press, London.

Koch, M., J. Bishop & T. Mitchell-Olds. 1999. Molecular systematics and evolution of *Arabidopsis* and *Arabis.* Pl. Biol. 1: 529–537.

———, B. Haubold & T. Mitchell-Olds. 2001. Molecular systematics of the Brassicaceae: Evidence from coding plastidic *mat*K and nuclear *Chs* sequences. Amer. J. Bot. 88: 534–544.

López Gonzalez, G. 1993. *Euzomodendron. In:* S. Castroviejo et al. (editors), Fl. Iberica 4: 344–346. Real Jardín Botánico, Madrid.

Marais, W. 1970. Cruciferae. *In:* L. E. Codd et al. (editors), Fl. Southern Africa 13: 1–118. Government Printer, Pretoria.

Poulter, B. A. 1956. The genus *Graellsia.* Notes Roy. Bot. Gard. Edinburgh 22: 85–93.

Raven, P. H. & D. I. Axelrod. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72: 1–134.

Rollins, R. C. 1963. The evolution and systematics of *Leavenworthia* (Cruciferae). Contr. Gray Herb. 192: 3–98.

———. 1969. A remarkable new crucifer from Mexico. Contr. Gray Herb. 198: 3–8.

———. 1993a. The Cruciferae of Continental North America. Stanford Univ. Press, Stanford.

———. 1993b. *Tropidocarpum.* Pp. 447–448 *in* J. C. Hickman (editor), The Jepson Manual. Univ. California Press, Berkeley.

Schulz, O. E. 1936. Cruciferae. *In:* A. Engler & H. Harms (editors), Die natürlichen Pflanzenfamilien, ed. 2, 17B: 227–658. Verlag von Wilhelm Engelmann, Leipzig.

Sytsma, K. J. & L. D. Gottlieb. 1986. Chloroplast DNA evidence for the origin of the genus *Heterogaura* from a species of *Clarkia* (Onagraceae). Proc. Natl. Acad. Sci. U.S.A. 83: 5554–5557.

Warwick, S. I. & I. A. Al-Shehbaz. 1998. Generic evaluation of *Boleum, Euzomodendron,* and *Vella* (Brassicaceae). Novon 8: 321–325.

——— & L. D. Black. 1994. Evaluation of the subtribes Moricandiinae, Savignyinae, Vellinae and Zillinae (Brassicaceae, tribe Brassiceae) using chloroplast DNA restriction site variation. Canad. J. Bot. 72: 1692–1701.